A general procedure for predicting rates of inbreeding in populations undergoing mass selection

A General Procedure for Predicting Rates of Inbreeding in Populations Undergoing Mass Selection

Piter Bijma,* Johan A. M. Van Arendonk* and John A. Woolliams†

**Animal Breeding and Genetics Group, Wageningen Institute of Animal Sciences, Wageningen Agricultural University, 6700 AH Wageningen, The Netherlands and †Roslin Institute (Edinburgh), Roslin, Midlothian EH25 9PS, United Kingdom*

Manuscript received March 30, 1999
Accepted for publication December 6, 1999

ABSTRACT

Predictions of rates of inbreeding (ΔF), based on the concept of long-term genetic contributions assuming the infinitesimal model, are developed for populations with discrete or overlapping generations undergoing mass selection. Phenotypes of individuals are assumed to be recorded prior to reproductive age and to remain constant over time. The prediction method accounts for inheritance of selective advantage both within and between age classes and for changing selection intensities with age. Terms corresponding to previous methods that assume constant selection intensity with age are identified. Predictions are accurate (relative errors $\leq$8%), except for cases with extreme selection intensities in females in combination with high heritability. With overlapping generations ΔF reaches a maximum when parents are equally distributed over age classes, which is mainly due to selection of the same individuals in consecutive years. ΔF/year decreases much more slowly compared to ΔF/generation as the number of younger individuals increases, whereas the decrease is more similar as the number of older individuals increases. The minimum ΔF (per year or per generation) is obtained when most parents were in the later age classes, which is mainly due to an increased number of parents per generation. With overlapping generations, the relationship between heritability and ΔF is dependent on the age structure of the population.

IN the absence of selection and with a Poisson distribution of family size, expected rates of inbreeding are related directly to the number of parents: $E(\Delta F) \approx 1/8N_m + 1/8N_f$ (Wright 1969, p. 212). In selected populations, however, superior families contribute more offspring to the next generation than average families. This increases the rate of inbreeding of a selected population compared to an unselected population. Prediction of rates of inbreeding in selected populations is difficult, because selection decisions are correlated over generations due to the inheritance of selective advantage. Methods accounting for only one or two generations of selection (*e.g.*, Burrows 1984a,b) therefore generally underestimate the rate of inbreeding (Wray *et al.* 1990; see Caballero 1994 for a review).

Two approaches to prediction of rates of inbreeding for selected populations can be distinguished. First, rates of inbreeding can be predicted on the basis of the variance of allele frequency, using the idea of accumulation of selective advantages over generations (Robertson 1961). Using this approach and equilibrium genetic variances, Santiago and Caballero (1995) obtained accurate predictions for populations with discrete generations under mass selection. Nomura (1996) extended that method to populations with overlapping generations and equal numbers of parents per sex in every age class. Second, rates of inbreeding can be predicted using the concept of long-term genetic contributions. Rates of inbreeding are proportional to the sum of squared long-term genetic contributions of ancestors (Wray and Thompson 1990). Wray and Thompson (1990) obtained accurate predictions of rates of inbreeding for populations with discrete generations under mass selection, using iterative regression methods. For discrete generations and mass selection a closed form expression was obtained by Woolliams *et al.* (1993). For more complicated selection schemes, however, predictions became unmanageable due to the recursive nature of the procedure and the need for predicting the variance of long-term genetic contributions (Wray *et al.* 1994).

Recently, Woolliams and Bijma (2000) showed that the variance of long-term genetic contributions is related to their squared expectation, making a separate prediction of the variance redundant. Furthermore, Woolliams *et al.* (1999) obtained general predictions of expected genetic contributions using equilibrium genetic variances instead of second generation genetic variances (Woolliams *et al.* 1993). Using the approach of Woolliams *et al.* (1999), Bijma and Woolliams (1999) obtained accurate predictions of genetic contributions for populations with overlapping generations under mass or sib-index selection. However, they did not develop predictions for rates of inbreeding for those schemes.

The aim of this article is twofold. First, explicit predic-

Corresponding author: Piter Bijma, Animal Breeding and Genetics Group, Department of Animal Sciences, Wageningen Agricultural University, P.O. Box 338, Marijkeweg 40, 6700 AH Wageningen, The Netherlands. E-mail: piter.bijma@alg.vf.wau.nl

tion equations for rates of inbreeding in populations with discrete or overlapping generations under mass selection are developed, on the basis of the theory of Woolliams *et al.* (1999) and Woolliams and Bijma (2000). These predictions are valid for any distribution of parents across age classes, overcoming the restriction of Nomura (1996), to give a general and practical method for mass selection with overlapping generations. These methods are compared to methods of Santiago and Caballero (1995) for discrete generations, and to methods of Nomura (1996) for the special case of equal numbers of parents per age class with overlapping generations. The accuracy of predictions is examined using simulation. Second, relationships between rates of inbreeding and genetic or population parameters are examined, and differences between populations with discrete and overlapping generations are presented and discussed.

DERIVATION OF EXPRESSIONS

Population model: This section describes the population and the selection procedures for which rates of inbreeding are predicted. This model is also used in the simulation. The trait considered is assumed to be determined by an infinite number of additive loci, each having an infinitesimal effect (infinitesimal model; Fisher 1918). Phenotypic values are the sum of additive genetic values (breeding values) and environmental values, $P = A + E$. A population with either discrete or overlapping generations under mass selection is modeled. With parents up to a maximum age of $c_{\max}$ there are $2c_{\max}$ categories, one for each sex and age of parent. Categories are indexed by k or by l, so $k = 1 \ldots c_{\max}$ are males, and $k = c_{\max}+1 \ldots 2c_{\max}$ are females. With discrete generations, there are only two categories: males and females that are indexed by $s = m$ or f. Before reproductive age, phenotypes of individuals are recorded and remain unchanged over time, so that ranking of individuals within categories is constant over time. Within categories, individuals are ranked on their phenotype and each year the highest-ranking n_k individuals are selected from the kth category, to produce the next cohort. The total number of male and female parents of each cohort is $N_m = \Sigma_{k=1}^{c_{\max}} n_k$ and $N_f = \Sigma_{k=c_{\max}+1}^{2c_{\max}} n_k$, respectively. Each sire is mated at random to d dams ($d = N_f/N_m$), and each dam produces a fixed number, n_o, of offspring ($\frac{1}{2}n_o$ of each sex), so that for each sex the total number of offspring born in a cohort is $T = \frac{1}{2}n_o N_f$. The unit of age, *i.e.*, the interval between consecutive age classes, was 1 year. Genetic contributions and rates of inbreeding per year therefore will be equal to genetic contributions and rates of inbreeding per cohort.

General: The prediction of ΔF is based on the concept of long-term genetic contributions (James and McBride 1958). The long-term genetic contribution (r_i) of ancestor i in cohort t_1 is defined as the proportion of genes present in individuals in cohort t_2 deriving by descent from i, where $(t_2 - t_1) \rightarrow \infty$ (Woolliams *et al.* 1993). In the remainder of the current article, long-term genetic contributions of ancestors are referred to as "genetic contributions," or simply as "contributions."

Rates of inbreeding are predicted from Woolliams and Bijma (2000),

$$E(\Delta F) \approx \tfrac{1}{2}\,\mathbf{1}^T\mathbf{N}E(\mathbf{u}^2) + \tfrac{1}{8}\mathbf{1}^T\mathbf{N}\boldsymbol{\delta}, \qquad (1)$$

where $\mathbf{1}^T = (1\ 1\ 1 \ldots 1)$, $\mathbf{N}$ is a $2c_{\max} \times 2c_{\max}$ diagonal matrix containing the numbers of parents selected from every category, $\mathbf{u}$ is a $2c_{\max}$ vector of expected lifetime long-term genetic contributions of parents, *i.e.*, $\mathbf{u}^2 = (u_{i,1}^2\, u_{i,2}^2 \ldots u_{i,2c_{\max}}^2)$, where $u_{i,s}$ is the expected *lifetime* long-term contribution of individual i in category s conditional on its selective advantage (which in mass selection is the breeding value), and $\boldsymbol{\delta}$ is a $2c_{\max}$ vector of correction factors for deviations of the variance of family size ($\mathbf{V}_n$) from independent Poisson variances. Throughout the article, family size refers to the number of selected offspring of a parent, not to the number of candidates. With mass selection and fixed n_o, $\boldsymbol{\delta}$ takes negative values, showing that ΔF for fixed n_o is less than for $n_o \sim$ Poisson. In Equation 1, categories are exclusive, *i.e.*, individuals are in only one category, and categories are therefore indexed by s instead of k. The scalar equivalent of Equation 1 is $E(\Delta F) = \frac{1}{2}\Sigma_s n_s E(u_{i,s}^2) + \frac{1}{8}\Sigma_s n_s \delta_s$, where Σ_s denotes summation over all exclusive categories.

To calculate $E(u_{i,s}^2)$, the selective advantage of the mate has to be included since the mate affects the contribution of an ancestor. With random mating and mass selection, however, the selective advantages of mates are independent and it is therefore possible to ignore the mate when calculating $u_{i,s}$ and add the mate term when calculating $E(u_{i,s}^2)$. The advantage of this is that the selective advantage contains only one term (the breeding value of the individual), which simplifies the prediction of $u_{i,k}$.

Rates of inbreeding are predicted in three steps. First, expected genetic contributions are predicted using the method of Woolliams *et al.* (1999). Second, $E(u_{i,s}^2)$ is derived and third, δ_s is derived. Discrete and overlapping generations are treated separately.

The difference between the current prediction and the method of Woolliams *et al.* (1993) is (1) the current prediction is based on equilibrium genetic variances, which simplifies the prediction of $u_{i,s}$ (Woolliams *et al.* 1999); (2) the variance of genetic contributions is not predicted separately, since it is related to the mean (Woolliams and Bijma 2000).

Discrete generations

Step 1: prediction of expected long-term genetic contributions: Expected genetic contributions of ancestors are obtained from the linear model (Bijma and Woolliams 1999),

$$E(r_{i,s}|A_{i,s}) = u_{i,s} = \alpha_s + \beta_s(A_{i,s} - \bar{A}_s), \quad (2)$$

where s denotes males or females, α_s is the expected contribution for an average ancestor of sex s, and β_s is the regression coefficient of the contribution on the breeding value ($A_{i,s}$) of the ancestor as a deviation from the average of the selected group ($\bar{A}_s$) for sex s. In discrete generations, $\alpha_s = 1/(2N_s)$ and $\beta_s = \alpha_s\lambda/(1 - \pi)$, where $\lambda = \frac{1}{2}i\sigma_P^{-1}$ is the average regression coefficient of the number of selected male and female offspring on the breeding value of the parent, and $\pi = \frac{1}{2}(1 - \kappa h^2)$ is the average regression coefficient of the breeding value of selected male and female offspring on the breeding value of the parent (Bijma and Woolliams 1999). Here, $i = \frac{1}{2}(i_m + i_f)$ is selection intensity, $\kappa = \frac{1}{2}(\kappa_m + \kappa_f)$ is Pearson's (1903) variance reduction coefficient, and $h^2 = \sigma_A^2/\sigma_P^2$, where σ_A^2 and σ_P^2 are Bulmer's (1971) equilibrium genetic and phenotypic variance.

Step 2: derivation of $E(u_{i,s}^2)$: Substituting Equation 2 and with terms added for the mate,

$$E(u_{i,m}^2) = \alpha_m^2 + \beta_m^2 E[(A_{i,m} - \bar{A}_m)^2] + \sum_{j=1}^{d}\beta_f^2 E[(A_{j,f} - \bar{A}_f)^2] \quad (3)$$

$$E(u_{i,f}^2) = \alpha_f^2 + \beta_f^2 E[(A_{i,f} - \bar{A}_f)^2] + \frac{1}{d^2}\beta_m^2 E[(A_{j,m} - \bar{A}_m)^2], \quad (4)$$

where j denotes the mate and

$$E[(A_{i,s} - \bar{A}_s)^2] = (1 - 1/N_s)\sigma_A^2(1 - \kappa_s h^2). \quad (5)$$

From Equation 1, ignoring the second term, $E(\Delta F) = \frac{1}{2}[N_m E(u_{i,m}^2) + N_f E(u_{i,f}^2)]$. From Equation 3 and 4 and the equations for β_s, λ, and π, predicted ΔF (see appendix a) is

$$E(\Delta F) = \frac{1}{8N_m} + \frac{1}{8N_f} + \frac{i^2h^2}{4(1 + \kappa h^2)^2}\left[(1 - \kappa_m h^2)\left(1 - \frac{1}{N_m}\right)\left(\frac{1}{2N_m} + \frac{1}{2N_f}\right) + (1 - \kappa_f h^2)\left(1 - \frac{1}{N_f}\right)\frac{1}{N_f}\right]. \quad (6)$$

For $N_m = N_f = \frac{1}{2}N$, the result simplifies to

$$E(\Delta F) = \frac{1}{2N} + \frac{1}{N}\left[\frac{i^2h^2(1 - \kappa h^2)(1 - 2/N)}{(1 + \kappa h^2)^2}\right]. \quad (7)$$

The assumption for Equations 6 and 7 is that, conditional on the selective advantage [*i.e.*, conditional on $(A_{i,s} - \bar{A}_s)$ in mass selection] family size follows a Poisson distribution (Woolliams and Bijma 2000), which is approximately the case with mass selection when $n_o \sim$ Poisson. A numerical example is in appendix a.

Step 3: Correction of $E(\Delta F)$ for deviations of $\mathbf{V}_n$ from Poisson variances: With fixed n_o, family size follows a hypergeometric distribution (Burrows 1984b) and a correction is required according to the second term of Equation 1. In this article, the hypergeometric variance is approximated by a binomial variance, which simplifies the prediction. For more complicated selection strategies, *e.g.*, index selection, a hypergeometric variance may be required (Woolliams and Bijma 2000).

With discrete generations, the second term of Equation 1 reduces to $\frac{1}{8}[N_m\delta_m + N_f\delta_f]$, where $\delta_s = \alpha^T\mathbf{V}_{n(s),dev}\alpha$, $\alpha^T = (\alpha_m\ \alpha_f)$ and $\mathbf{V}_{n(s),dev}$ is the 2×2 matrix of deviations of the (co)variance of family size from Poisson variances for sex s (Woolliams and Bijma 2000). Diagonal elements of $\mathbf{V}_{n(s),dev}$ are obtained as $\mathbf{V}_{n(s),dev} = \mathbf{V}_{n(s)} - \mathbf{V}_{n(s),Poisson}$, which are of the form $np(1 - p) - np = -np^2$, where n is the number of candidates and p is the selected proportion. Off-diagonal elements of $\mathbf{V}_{n(s),dev}$ are zero. For discrete generations the total correction (appendix a) equals

$$\tfrac{1}{8}\mathbf{1}^T\mathbf{N}\boldsymbol{\delta} = \frac{-1}{8T}. \quad (8)$$

Relation to Santiago and Caballero (1995): The prediction equation of Santiago and Caballero (1995) can be related directly to the current prediction. With random mating and assuming $\alpha_{I,s} = \alpha_O = 0$ (see Santiago and Caballero 1995 for notation), Equations 21 and 36 of Santiago and Caballero (1995) reduce to $\frac{1}{2}N_m[\alpha_m^2 + \alpha_m^2Q^2C_m^2] + \frac{1}{2}N_f[\alpha_f^2 + \alpha_f^2Q^2C_f^2]$ (Bijma *et al.* 1999). This can be equated directly to the first term of Equation 1, which shows that $E(u_{i,s}^2)$ corresponds to $[\alpha_s^2 + \alpha_s^2Q^2C_s^2]$, and also that $\alpha_s^2Q^2C_s^2$ corresponds to $\beta_s^2E[(A_{i,s} - \bar{A}_s)^2]$. Santiago and Caballero (1995) use $Q = 1/[1 - \frac{1}{2}(1 - \kappa h^2)]$, which is identical to our $1/(1 - \pi)$. Furthermore, they use $C_s^2 = \frac{1}{2}i^2h^2(1 - \kappa h^2)$, which is identical to our $2\lambda^2E[(A_{i,s} - \bar{A}_s)^2]$, where the 2 accounts for the mate.

The correction for deviations of $\mathbf{V}_n$ from Poisson variances can also be related to Equation 36 of Santiago and Caballero (1995). They use $\mathbf{V}_{n(s)}(s',s') = N_{s'}/N_s[1 - N_{s'}/\tilde{n}_sN_s]$ (see Santiago and Caballero 1995, Equation 30 and ignore the term C_{sm}^2), where $\tilde{n}_s$ is the number of selection candidates per sex of a parent of sex s ($\tilde{n}_m = \frac{1}{2}n_od$, $\tilde{n}_f = \frac{1}{2}n_o$) and s' denotes the sex of the offspring. This is a binomial variance. The deviation from a Poisson variance (*i.e.*, $N_{s'}/N_s$) equals $\mathbf{V}_{n(s),dev}(s', s') = N_{s'}^2/(N_s^2\tilde{n}_s)$. From Equation 36 of Santiago and Caballero (1995), the total correction of ΔF equals $-\frac{1}{8}T^{-1}$, which is identical to Equation 8 (Bijma *et al.* 1999). Therefore, Equations 21, 30, and 36 of Santiago and Caballero (1995) are identical to the current prediction for mass selection. A numerical difference between both methods exists because Santiago and Caballero (1995) omit the correction for a finite number of parents when calculating their $C_{ss'}^2$, which would be equivalent to omitting the $(1 - 1/N_s)$ in Equation 5 of the current prediction.

Overlapping generations

Step 1: prediction of expected long-term genetic contributions: Genetic contributions are predicted using Equation 2 again, but now categories refer to sex-age class combinations, which are indexed by k instead of s, so that $k = 1 \ldots 2c_{max}$ and $u_{i,k}$ is the expected genetic contribution of individual i originating from its selection in category k. Solutions for α_k and β_k are obtained from Woolliams *et al.* (1999),

$$\mathbf{N\alpha} = [\mathbf{G}^T + (\mathbf{G}^T * \mathbf{D}^T)(\mathbf{I} - \mathbf{G}^T * \mathbf{\Pi}^T)^{-1}(\mathbf{G}^T * \mathbf{\Lambda}^T)]\mathbf{N\alpha} \tag{9}$$

$$\mathbf{N\beta} = (\mathbf{I} - \mathbf{G}^T * \mathbf{\Pi}^T)^{-1}(\mathbf{G}^T * \mathbf{\Lambda}^T)(\mathbf{N\alpha}), \tag{10}$$

where * denotes element-by-element multiplication, T denotes the transpose of matrices, $\mathbf{I}$ is the $2c_{max} \times 2c_{max}$ identity matrix, $\mathbf{N}$ is a $2c_{max} \times 2c_{max}$ diagonal matrix containing the numbers of parents selected from every category (n_k), Π is a $2c_{max} \times 2c_{max}$ matrix with each element, π_{kl}, being the regression coefficient of the breeding value of a selected offspring in category k on the breeding value of the parent in category l, Λ is a $2c_{max} \times 2c_{max}$ matrix with each element, λ_{kl}, being the regression coefficient of the number of selected offspring in category k on the breeding value of the parent in category l, $\mathbf{G}$ is a $2c_{max} \times 2c_{max}$ modified gene flow matrix connecting selected offspring to parental categories, $\mathbf{D}$ is a $2c_{max} \times 2c_{max}$ matrix of deviations of breeding values from the mean of the selected group, $\boldsymbol{\alpha}$ is a $2c_{max}$ vector of elements α_l, and $\boldsymbol{\beta}$ is a $2c_{max}$ vector of elements β_l. Generation interval (L) was calculated as the time interval in which genetic contributions sum to 1: $L = 1/[\Sigma_{k=1}^{2c_{max}} n_k\alpha_k]$ (Woolliams *et al.* 1999). More details and a numerical example are in Bijma and Woolliams (1999).

Contributions predicted from Equations 9 and 10 are per year; *i.e.*, they are the long-term contribution of a single cohort, not of a total generation. Rates of inbreeding predicted from these contributions therefore are also per year.

Step 2: derivation of $E(u_{i,s}^2)$: For the calculation of $E(u_{i,s}^2)$ one needs to find the *lifetime* expected genetic contribution; *i.e.*, one has to account for the fact that individuals may be selected in multiple categories. With c_{max} age classes per sex and the ranking of individuals within age classes remaining constant, there are $2c_{max}$ exclusive categories, which will be indexed by s, *i.e.*, individuals selected once, twice, up to c_{max} times for each sex. Therefore, $s = 1 \ldots c_{max}$ denotes males selected 1 through c_{max} times and $s = c_{max}+1 \ldots 2c_{max}$ denotes females selected 1 through c_{max} times. The expected lifetime contribution for these categories is $u_{i,s} = \Sigma_k u_{i,k}$, where the sum is taken over the age-sex categories k from which i is selected. Thus individuals are indexed in two different ways, *i.e.*, by whether or not they were selected at a specific age, denoted by k, and by how many times they were selected throughout their lifetime, denoted by s.

The scalar equivalent of the first term of Equation 1 is

$$\tfrac{1}{2}\sum_{s=1}^{c_{max}} n_s E(u_{i,s}^2) + \tfrac{1}{2}\sum_{s=c_{max}+1}^{2c_{max}} n_s E(u_{i,s}^2),$$

with the first term denoting males and the second females. The summation over exclusive categories s can be written in terms of the categories k, for males,

$$\sum_{s=1}^{c_{max}} n_s E(u_{i,s}^2) = \sum_{k=1}^{c_{max}} n_k E(u_{i,k}^2) + 2\sum_{k=1}^{c_{max}-1}\sum_{l=k+1}^{c_{max}} \min(n_l, n_k) E(u_{i,k}u_{i,l}), \tag{11}$$

and for females,

$$\sum_{s=c_{max}+1}^{2c_{max}} n_s E(u_{i,s}^2) = \sum_{k=c_{max}+1}^{2c_{max}} n_k E(u_{i,k}^2) + 2\sum_{k=c_{max}+1}^{2c_{max}-1}\sum_{l=k+1}^{2c_{max}} \min(n_k, n_l) E(u_{i,k}u_{i,l}), \tag{12}$$

where $\min(n_k,n_l)$ denotes the minimum of n_k and n_l (see also example in appendix b). These summations can be written in matrix form, so that for Poisson family size, the rate of inbreeding per year is

$$E(\Delta F_Y) = \tfrac{1}{2}\mathbf{1}^T\mathbf{N}_o\mathbf{U}_o\mathbf{1}, \tag{13}$$

where $\mathbf{1} = (1\ 1 \ldots 1)^T$, $\mathbf{N}_o$ is similar to $\mathbf{N}$ but has a reordering of age classes within sexes so that they go from large to small according to the number of parents, and $\mathbf{U}_o$ is a $2c_{max} \times 2c_{max}$ matrix containing a lower triangular submatrix for each sex (with categories ordered as in $\mathbf{N}_o$), with $E(u_{i,k}^2)$ on the diagonal and $2E(u_{i,k}u_{i,l})$ as off-diagonals in the lower triangular submatrices (see example in appendix b). Note that, although Equation 1 uses exclusive categories s, we have expressed ΔF_Y in terms of the age-sex categories k in Equation 13. Thus, the expected genetic contributions for the categories k can be used directly in Equation 13. Rates of inbreeding per generation were calculated as $E[\Delta F_L] = LE[\Delta F_Y]$.

As with discrete generations, $E(u_{i,k}^2)$ has to include terms for the mates. With overlapping generations, the mate term consists of two elements. The first element is due to the category of the mate as a deviation of the average category for the sex of the mate, $\alpha_l - \overline{\alpha}_{sex(l)}$. The second term is due to the selective advantage of the mate within its category, $\beta_l(A_{i,l} - \overline{A}_l)$. Therefore, for males, $u_{i,k} = \alpha_k + \beta_k(A_{i,k} - \overline{A}_k) + \Sigma_{j=1}^{d}[(\alpha_l - \overline{\alpha}_{sex(l)}) + \beta_l(A_{j,l} - \overline{A}_l)]$; and for females, $u_{i,k} = \alpha_k + \beta_k(A_{i,k} - \overline{A}_k) + [(\alpha_l - \overline{\alpha}_{sex(l)}) + \beta_l(A_{j,l} - \overline{A}_l)]/d$, where j denotes the mate, l the category of the mate, and sex the sex of the mate. For Equations 11 and 12, expectations of squared contributions are obtained for males as

$$E(u_{i,k}^2) = \alpha_k^2 + (1 - 1/n_k)\beta_k^2\sigma_A^2(1 - \kappa_k h^2) + d\{\overline{\alpha_f^2} - \overline{\alpha}_f^2 + \sigma_A^2\overline{[(1 - 1/n_l)\beta_l^2(1 - \kappa_l h^2)]}_f\}, \quad (14)$$

where $k = 1 \ldots c_{max}$, and for females as

$$E(u_{i,k}^2) = \alpha_k^2 + (1 - 1/n_k)\beta_k^2\sigma_A^2(1 - \kappa_k h^2) + \frac{1}{d^2}\{\overline{\alpha_m^2} - \overline{\alpha}_m^2 + \sigma_A^2\overline{[(1 - 1/n_l)\beta_l^2(1 - \kappa_l h^2)]}_m\}, \quad (15)$$

where $k = c_{max}+1 \ldots 2c_{max}$ and bars with subscripts m or f denote weighted averages over mate categories.

Cross-products in Equations 11 and 12 arise only from the individuals selected in both categories, which are all the individuals selected from the smallest category [*i.e.*, $\min(n_k,n_l)$]. Cross-products are therefore

$$E(u_{i,k}u_{i,l}) = \alpha_k\alpha_l + [1 - 1/\min(n_l, n_k)]\beta_k\beta_l\sigma_A^2[1 - \max(\kappa_k, \kappa_l)h^2] + \alpha_{min}\beta_{max}E[\bar{A}_{min} - \bar{A}_{max}], \quad (16)$$

where subscript min denotes the category with the lower number of parents and subscript max denotes the category with the higher number of parents. (With random mating there is no covariance between different mates of *i*; therefore, there is no mate term in the cross-product.) A numerical example is in appendix b.

Step 3: correction of $E(\Delta F_y)$ for deviations of $\mathbf{V}_n$ from Poisson variances: The second term of Equation 1 is $\frac{1}{8}\mathbf{1}^T\mathbf{N}\boldsymbol{\delta}$, where $\boldsymbol{\delta}$ is a $2c_{max}$ vector of elements $\delta_k = \alpha^T\mathbf{V}_{n(k),dev}\alpha$, and $\mathbf{V}_{n(k),dev}$ is a $2c_{max} \times 2c_{max}$ matrix with deviations from Poisson variances (Woolliams and Bijma 2000). Similar to the discrete generation case, $\mathbf{V}_{n(k)}$ is approximated by a binomial variance. Elements of $\mathbf{V}_{n(k),dev}$ and a numerical example are in appendix b.

Relation to Nomura (1996): Nomura (1996) developed predictions for the special case of equal numbers of parents per sex selected from every age class (denoted n_m and n_f), *i.e.*, for constant selection intensity with age. With those schemes every parent is selected in every category (except for categories with zero parents) and there are only two exclusive categories; *i.e.*, males selected always and females selected always. In this respect, schemes with equal numbers of parents selected from every age class are like discrete generations, *i.e.*, only two categories that do not compete for being selected. Bijma *et al.* (1999) show that Equations 30 and 31 of Nomura (1996) reduce to $\Delta F_Y = \frac{1}{2}n_m[\alpha_m^2 + \alpha_m^2Q^2C_m^2] + \frac{1}{2}n_f[\alpha_f^2 + \alpha_f^2Q^2C_f^2]$, which is equivalent to the first term of Equation 1. This result is a rescaling of discrete generations, *i.e.*, with discrete generation $\alpha_s = 1/(2N_s)$, with overlapping generations and two exclusive categories, each contributing half, $\alpha_s = 1/(2n_sL)$, where L is the generation interval. Summation of contributions over the number of parents per generation shows that they sum to unity:

$$\sum_{i=1}^{n_mL} 1/(2N_mL) + \sum_{i=1}^{n_fL} 1/(2N_fL) = 1.$$

Furthermore, Nomura (1996) calculated Q using $(\mathbf{I} - \mathbf{P})^{-1}$ [$\mathbf{P}$ is a gene flow matrix identifying the contribution of parental age groups to selected offspring multiplied by the proportion of genetic variance remaining after selection; Nomura (1996, Appendix)], which, for his special case, is equivalent to our $(\mathbf{I} - \mathbf{G}^T*\Pi^T)^{-1}$ (see Woolliams *et al.* 1999, Equation 10). Analogous to Santiago and Caballero (1995), Nomura (1996) calculated C_s^2 omitting the $(1 - 1/n_s)$. Contrary to Santiago and Caballero (1995) and to the present study, Nomura (1996) included a term $C_{ss'}^2$ in the calculation of $\mathbf{V}_{n(s)}$ [first term in Equation 22 of Nomura (1996)]. Finally, Nomura (1996) considered only one generation inheritance of selective advantage when he calculated the total contribution of age classes. [See Equation 8 of Nomura (1996), which is equivalent to solving α from $\mathbf{N}\alpha = \mathbf{G}^T\mathbf{N}\alpha$ instead of using Equation 9 (Woolliams *et al.* 1999).]

Stochastic simulation: To examine the accuracy of the prediction equations, the breeding scheme described in the "population model" section was simulated and rates of inbreeding were calculated from simulated data. The simulation procedure is described in Bijma and Woolliams (1999). In the simulated data, an ancestor cohort t_1 and a descendent cohort t_2 were chosen (Bijma and Woolliams 1999). Inbreeding coefficients of individuals in cohorts t_1 and t_2 were calculated from the simulated pedigree, using the algorithm of Meuwissen and Luo (1992). Rates of inbreeding per year were calculated as $\Delta F_y = 1 - [(1 - \bar{F}_{t2})/(1 - \bar{F}_{t1})]^{(t_2-t_1)^{-1}}$, where $\bar{F}_{t_1}$ and $\bar{F}_{t_2}$ are the average inbreeding coefficients in cohorts t_1 and t_2, respectively. Rates of inbreeding per generation were calculated as $\Delta F_L = L\Delta F_y$. Results were averaged over 500 replicates.

RESULTS

Discrete generations: For examination of the accuracy of predictions and to identify the origin of prediction errors, Table 1 shows simulated and predicted ΔF. Two types of predictions are in Table 1: ΔF_{pred}* is the prediction using α and β estimated from simulation, and ΔF_{pred} is the full deterministic prediction using α and β from Equations 9 and 10. Differences between ΔF_{pred} and ΔF_{pred}* reflect prediction errors originating from the prediction of β [in discrete generations, $\alpha_s = 1/(2N_s)$ is known]. Differences between ΔF_{sim} and ΔF_{pred}* reflect errors in Equation 1.

Generally, errors of the full prediction in Table 1 are small, most errors are below 5%, maximum errors are up to 8.1%, and trends agree well between simulations and predictions. Though errors are small, some trends can be observed. Most errors are positive and errors tend to be highest for $N_m = 10$, but errors tend to be

TABLE 1

Rates of inbreeding from simulation (ΔF_{sim}) and from prediction (ΔF_{pred}*, ΔF_{pred}) for populations with discrete generations

		$h^2 = 0.2$						$h^2 = 0.5$					
		$n_o = 4$			$n_o = 8$			$n_o = 4$			$n_o = 8$		
N_m	d	ΔF_{sim}	ΔF_{pred}*	ΔF_{pred}	ΔF_{sim}	ΔF_{pred}*	ΔF_{pred}	ΔF_{sim}	ΔF_{pred}*	ΔF_{pred}	ΔF_{sim}	ΔF_{pred}*	ΔF_{pred}
10	1	0.0222	0.0225	0.0225	0.0291	0.0300	0.0306	0.0235	0.0243	0.0243	0.0323	0.0323	0.0339
	2	0.0186	0.0195	0.0195	0.0226	0.0230	0.0244	0.0204	0.0208	0.0211	0.0261	0.0265	0.0269
	5	0.0166	0.0173	0.0174	0.0191	0.0196	0.0203	0.0179	0.0185	0.0187	0.0216	0.0210	0.0222
40	1	0.0056	0.0057	0.0057	0.0077	0.0078	0.0078	0.0059	0.0062	0.0062	0.0086	0.0087	0.0087
	2	0.0047	0.0049	0.0049	0.0062	0.0061	0.0062	0.0052	0.0054	0.0054	0.0071	0.0069	0.0069
	5	0.0043	0.0043	0.0044	0.0053	0.0051	0.0052	0.0048	0.0048	0.0048	0.0061	0.0057	0.0057
100	1	0.0022	0.0023	0.0023	0.0031	0.0031	0.0032	0.0024	0.0025	0.0025	0.0036	0.0036	0.0035
	2	0.0019	0.0020	0.0020	0.0025	0.0025	0.0025	0.0021	0.0022	0.0022	0.0029	0.0028	0.0028
	5	0.0017	0.0018	0.0018	0.0022	0.0021	0.0021	0.0019	0.0019	0.0020	0.0025	0.0023	0.0023

ΔF_{pred}*, prediction using α and β from simulation; ΔF_{pred}, full prediction; h_0^2, base generation heritability; N_m, no. of selected sires; d, mating ratio; n_o, number of offspring per dam. Standard errors of simulation result were ~1% of the estimate.

negative for $n_o = 8$ and $N_m = 100$. Prediction errors are partly due to errors in the prediction of β; *i.e.*, ΔF_{pred}* is generally more accurate than ΔF_{pred}. Because we have approximated the hypergeometric variance of family size by a binomial variance, positive errors for small numbers of parents were expected. The correction for hypergeometric variances becomes larger with fewer parents (Burrows 1984b), whereas a binomial correction is unaffected by the number of parents. Because the correction is a negative value, a binomial correction results in an overprediction for small numbers of parents. The current prediction was compared to the prediction of Santiago and Caballero (1995). As expected from the close agreement between equations of both methods, both methods gave very similar results (Bijma *et al.* 1999).

Figure 1 shows the relationship between ΔF and heritability (h_0^2), for $N_m = N_f = 20$ and for three selection intensities ($n_o = 2$, 8, or 32 $\rightarrow$ $i = 0$, 1.271, or 1.967). Though relationships of ΔF with heritability and selection intensity can be inferred from other studies (*e.g.*, Wray and Thompson 1990), they have never been explored in detail.

Figure 1 shows that ΔF has a maximum for intermediate heritabilities (except for $n_o = 2$), and changes in ΔF are more pronounced with greater selection intensity. The maximum of ΔF for intermediate h^2 is due to the Bulmer effect. When the Bulmer effect is ignored in Equation 7 (*i.e.*, $\kappa = 0$) the rate of inbreeding increases with h^2 over the whole range. The logic behind this is that with increasing h^2 the reduction of between-family variance increases, reducing the importance of the family component in the phenotype. [Note also that the intraclass correlation between full sibs [$\rho = \frac{1}{2}h^2(1 - \kappa h^2)$] has a maximum for $h^2_{max} = 1/(2\kappa)$, which for a common value of $\kappa = 0.8$ equals $h^2_{max} = 0.625$]. For $h_0^2 = 0$ and with Poisson family size, Equation 1 reduces to $E[\Delta F] = 1/(8N_m) + 1/(8N_f) = 0.0125$ (Wright 1969, p. 212).

With $n_o = 2$, one male and one female offspring are selected from every pair of parents, which gives zero variance of family size, $\beta = 0$, and minimal inbreeding. Expected long-term genetic contributions are equal for all parents and the variance of the contributions is zero; *i.e.*, expected and realized contributions are equal. The absence of variance of family size with $n_o = 2$ is taken into account by the correction of ΔF for deviations of $\mathbf{V}_n$

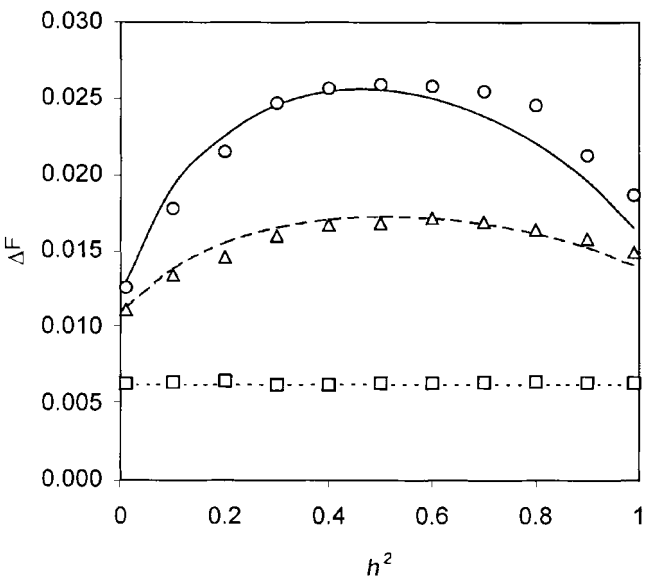

Figure 1.—Relation of predicted (lines) and simulated (symbols) rates of inbreeding (ΔF) with heritability (h_0^2) for populations with discrete generations, with 20 sires and 20 dams and varying number of offspring per dam (n_o). $n_o = 2$: □, ΔF_{sim}; · · ·, ΔF_{pred}. $n_o = 8$: △, ΔF_{sim}; - - -, ΔF_{pred}. $n_o = 32$: ○, ΔF_{sim}; —, ΔF_{pred}.

TABLE 2

Rates of inbreeding per generation from simulation (ΔF_{sim}) and from prediction (ΔF_{pred}) and generation intervals from simulation (L_{sim}) and prediction (L_{pred}) for populations with overlapping generations

	$h_0^2 = 0.2$				$h_0^2 = 0.5$			
diag N	ΔF_{Lsim}	ΔF_{Lpred}	L_{sim}	L_{pred}	ΔF_{Lsim}	ΔF_{Lpred}	L_{sim}	L_{pred}
1. {20, 0, 20, 0}	0.0150	0.0156	1.00	1.00	0.0169	0.0173	1.00	1.00
2. {20, 0, 15, 5}	0.0178	0.0185	1.11	1.11	0.0200	0.0207	1.10	1.10
3. {20, 0, 10, 10}	0.0194	0.0206	1.23	1.22	0.0229	0.0235	1.20	1.18
4. {20, 0, 5, 15}	0.0158	0.0165	1.35	1.34	0.0205	0.0209	1.32	1.30
5. {20, 0, 0, 20}	0.0097	0.0104	1.50	1.50	0.0112	0.0115	1.50	1.50
6. {20, 0, 0, 40}	0.0080	0.0083	1.50	1.50	0.0091	0.0091	1.50	1.50
7. {10, 10, 10, 10}	0.0237	0.0247	1.48	1.43	0.0285	0.0290	1.41	1.36
8. {19, 1, 38, 2}	0.0132	0.0133	1.05	1.05	0.0152	0.0148	1.04	1.04
9. {18, 2, 33, 7}[a]	0.0117	0.0123	1.14	1.13	0.0133	0.0137	1.13	1.13
10. {20, 0, 0, 10, 0, 30}	0.0103	0.0106	1.63	1.62	0.0163	0.0159	1.48	1.43
11. {20, 0, 0, 30, 0, 10}	0.0125	0.0130	1.17	1.16	0.0153	0.0150	1.10	1.10
12. {10, 5, 5, 0, 20, 10, 5, 5}	0.0217	0.0217	1.66	1.58	0.0267	0.0254	1.46	1.41

For $n_o = 8$, **N** is the distribution of parents over age classes and h_0^2 is the base generation heritability. Standard errors of ΔF_{sim} were ~1% of the estimate.

[a] $n_o = 4$ for this scheme.

from Poisson variances. Without this correction, ΔF_{pred} is equal to a situation with $h_0^2 = 0$ and Poisson family size, resulting in $\Delta F_{pred} = 0.0125$. The correction halves the prediction to 0.00625. This is an established result (Falconer and Mackay 1996, p. 69). In the absence of variance of family size (which can only be achieved for $d = 1$), effective population size equals twice the actual population size: $N_e = 2(N_m + N_f)$ and $E(\Delta F) = \frac{1}{2}N_e = 1/(4*40) = 0.00625$.

With higher selection intensities ($n_o = 8$ or 32), ΔF increases considerably with heritability. For example, for $h^2 = 0.6$, ΔF increases by 54% compared to random selection (*i.e.*, $h^2 = 0$) for $n_o = 8$, and by 105% for $n_o = 32$. The large increase of ΔF with selection intensity originates from the regression of the number of selected offspring on the breeding value of the parent, which is linear in i ($\lambda = \frac{1}{2}i\sigma_P^{-1}$), giving a quadratic term in ΔF (Equation 7). Large values of λ indicate that the population descends for a large proportion from only a few ancestors.

For practical selection intensities ($n_o = 2, 8$), there is close agreement between ΔF_{pred} and ΔF_{sim}. For large selection intensities errors are larger (*e.g.*, for $n_o = 200$, $N_m = N_f = 40$ and $h^2 = 0.4$, an error of −18% was found). Large errors for extreme selection intensities do not undermine the general theory, *i.e.*, Equation 1 is still valid, but the linear model (Equation 2) may be insufficient to predict expected genetic contributions (Woolliams and Bijma 2000).

Overlapping generations: Table 2 shows simulated and predicted rates of inbreeding per generation and generation intervals. Predictions of ΔF using α and β from simulation (such as ΔF_{pred}* in Table 1) are not included, because standard errors on β were too large to draw conclusive inferences. Because the potential number of alternative schemes is very large with overlapping generations, a wide range of schemes was evaluated. Only schemes 1, 3, 5, 6, and 7 are within the scope of Nomura (1996). Schemes 1–5 represent a situation with two age classes with gradually increasing ages of females. Scheme 6 is similar to scheme 5 but with a mating ratio of two. Scheme 7 has equal numbers of parents in all categories. With schemes 8 and 9, parents were ranked on estimated breeding value [$EBV_{i,k} = h^2(P_{i,k} - \bar{P}_k)$] across age classes and the highest ranking N_m males and N_f females were selected across age classes, which gives the highest genetic level of the offspring in the next cohort (James 1987). This strategy resulted in **N** = diag{19, 1, 38, 2} for $n_o = 8$ and **N** = diag{18, 2, 33, 7} for $n_o = 4$ (for both $h_0^2 = 0.2$ and 0.5). Furthermore, some arbitrary schemes with three and four age classes were evaluated to show that predictions are also accurate for more than two age classes. Prediction errors of ΔF_L were small, with most <5%. The maximum error was 6.6% and most errors were positive. Similar to the case with discrete generations, positive errors for small numbers of parents were expected due to the binomial approximation for the variance of family size.

Generation intervals are systematically underpredicted in Table 2 (except for schemes with only one reproductive category per sex in which case L is fixed; schemes 1, 5, and 6). The underprediction is entirely explained by the way L_{sim} is calculated, *i.e.*, $L_{sim} = 1/n_{repl}\sum_{k=1}^{n_{repl}} L_k$, where, $L_k = 1/\sum_{l=1}^{2c\,max} n_l\alpha_l$; *i.e.*, the generation interval is calculated per replicate as the time in which genetic contributions sum to unity and subsequently averaged over replicates (Bijma and Woolliams 1999). However, if α was averaged over replicates

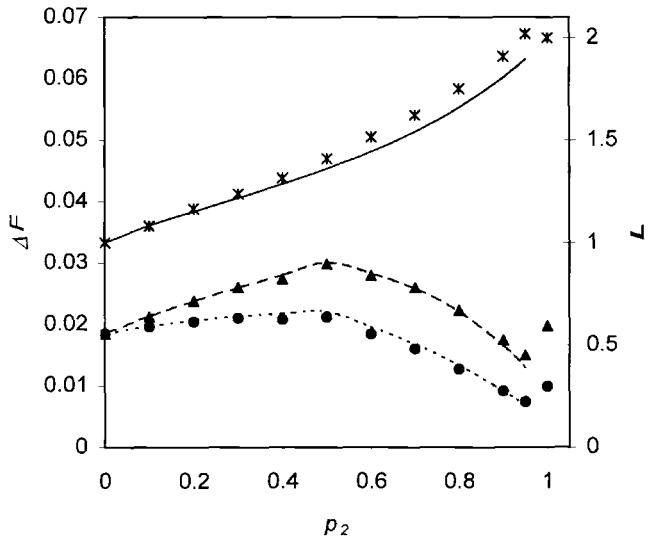

Figure 2.—Relation of the proportion of parents from the second age class (p_2) with predicted (lines) and simulated (symbols) generation intervals (L) and with rates of inbreeding per year (ΔF_γ), and per generation (ΔF_L), for a population with two age classes, $N_m = 20$, $N_f = 20$, $h_0^2 = 0.4$, and $n_o = 10$. ●, $\Delta F_{\gamma,sim}$; · · ·, $\Delta F_{\gamma,pred}$; ▲, $\Delta F_{L,sim}$; - - -, ΔF_{Lpred}; *, L_{sim}; —, L_{pred}.

and L_{sim} was calculated from the average, *i.e.*, $L_{sim} = 1/\Sigma_{k=1}^{2c\,max} n_k \bar{\alpha}_k$, then L_{pred} and L_{sim} were in very close agreement (results not shown). This result was expected from the nonlinear relationship between L and α, so that $E[L]$ differs from $1/\Sigma_{k=1}^{2c\,max} n_k E[\alpha_k]$.

Results from the current prediction were compared to results from the prediction of Nomura (1996) for the special case of equal numbers of parents selected from every age class. [A comparison was made for all schemes presented by Nomura (1996).] As expected from theory, results from both methods were similar (Bijma *et al.* 1999).

Relationship between ΔF and distribution of parents over age classes: Figure 2 shows the relationship between the rate of inbreeding (per year and per generation) and the proportion of parents selected from the second age class (p_2), for a population with two age classes, $N_m = N_f = 20$, $h_0^2 = 0.4$, and $n_o = 10$. With the exception of $p_2 = 0$, 0.5, and 1.0, these schemes are beyond the scope of Nomura (1996). Generation interval was also included in Figure 2. On the horizontal axis, parents are shifted from all parents in the first age class ($p_2 = 0$, $\mathbf{N} = \text{diag}\{20, 0, 20, 0\}$) to all parents in the second age class ($p_2 = 1$, $\mathbf{N} = \text{diag}\{0, 20, 0, 20\}$). For $p_2 = 1$, no predictions are presented (*i.e.*, no lines, only symbols), because in this scheme there are two distinct subpopulations that do not mix; *i.e.*, individuals born in odd-numbered cohorts are one population and individuals born in even-numbered cohorts are the other population. This scheme violates the assumption of one random mating population in the derivation of ΔF_{pred}. Therefore, the populations should be treated separately, which resulted in accurate predictions. Despite the complex relationship between ΔF and p_2 in Figure 2, where, for example, ΔF_γ is nearly constant before declining sharply, accurate predictions were obtained throughout. The rate of inbreeding per year has a flat curve with a maximum for $p_2 = 0.5$, because the increase of ΔF_L with p_2 is counteracted by an increase in the generation interval, and as a result, $\Delta F_\gamma = \Delta F_L / L$ shows only slight increase before $p_2 = 0.5$ and steep decrease after $p_2 = 0.5$.

For random selection, Hill (1979) showed that the rate of inbreeding in overlapping generations is related to the lifetime variance of family size and the number of parents entering the population per generation. The same pattern can be observed in Figure 2, which shows that ΔF_L has a maximum when parents are equally distributed over age classes, *i.e.*, for $\mathbf{N} = \text{diag}\{10, 10, 10, 10\}$, where the 10 parents selected in age class 1 the first year are the same as the 10 parents selected in age class 2 the next year. Thus only 10 distinct parents are selected from every cohort for this scheme, and with $L = 1.41$ the number of parents entering the population per generation equals only 14.1. For $\mathbf{N} = \text{diag}\{20, 0, 20, 0\}$, 20 distinct parents are selected from every cohort and with $L = 1$, 20 parents enter the population per generation. The rate of inbreeding per generation reaches a minimum for $p_2 = 0.95$ ($\mathbf{N} = \text{diag}\{1, 19, 1, 19\}$). At first glance, this result is counterintuitive; *i.e.*, one might expect approximately equal rates of inbreeding per generation for $\mathbf{N} = \text{diag}\{19, 1, 19, 1\}$ and for $\mathbf{N} = \text{diag}\{1, 19, 1, 19\}$. However, for $\mathbf{N} = \text{diag}\{1, 19, 1, 19\}$, 19 distinct individuals are selected from every cohort and, with $L = 1.90$, the number of parents per generation equals 36.1.

Line subdivision and migration: As mentioned earlier, the scheme with $\mathbf{N} = \text{diag}\{0, 20, 0, 20\}$ has two nonmixing lines. Changing this scheme to $\mathbf{N} = \text{diag}\{1, 19, 1, 19\}$ is equivalent to allowing some migration between both lines. Figure 3 shows a comparison between full line subdivision, line subdivision with migration, and one single line for schemes with 2 or 3 age classes. Note that the total number of parents per year is equal per comparison. The comparison shows that allowing some migration between lines substantially reduces ΔF_L (*i.e.*, 0.0104 *vs.* 0.0141 and 0.0075 *vs.* 0.0141). The smallest ΔF is obtained when lines are joined together ({40, 40} with a cohort interval of 2 years and {60, 60} with a cohort interval of 3 years). When comparing these rates of inbreeding, it must be realized, however, that the schemes with full line subdivision accumulate a between-line genetic variance equal to $2(1 - 1/n_{lines})F\sigma_{A0}^2$, where the $(1 - 1/n_{lines})$ accounts for the fact that the mean is estimated from the sample; *i.e.*, the variance is the observed variance in the sample (Falconer and Mackay 1996, p. 265). The total genetic variance at time t, *i.e.*, $\sigma_{A,t}^2 = \sigma_{A,between}^2 + \sigma_{A,within}^2$, equals σ_{A0}^2 for $\mathbf{N} = \text{diag}\{0, 20, 0, 20\}$ and $\sigma_{A0}^2(1 + \frac{2}{3}F_t)$ for $\mathbf{N} = \text{diag}\{0, 0,$

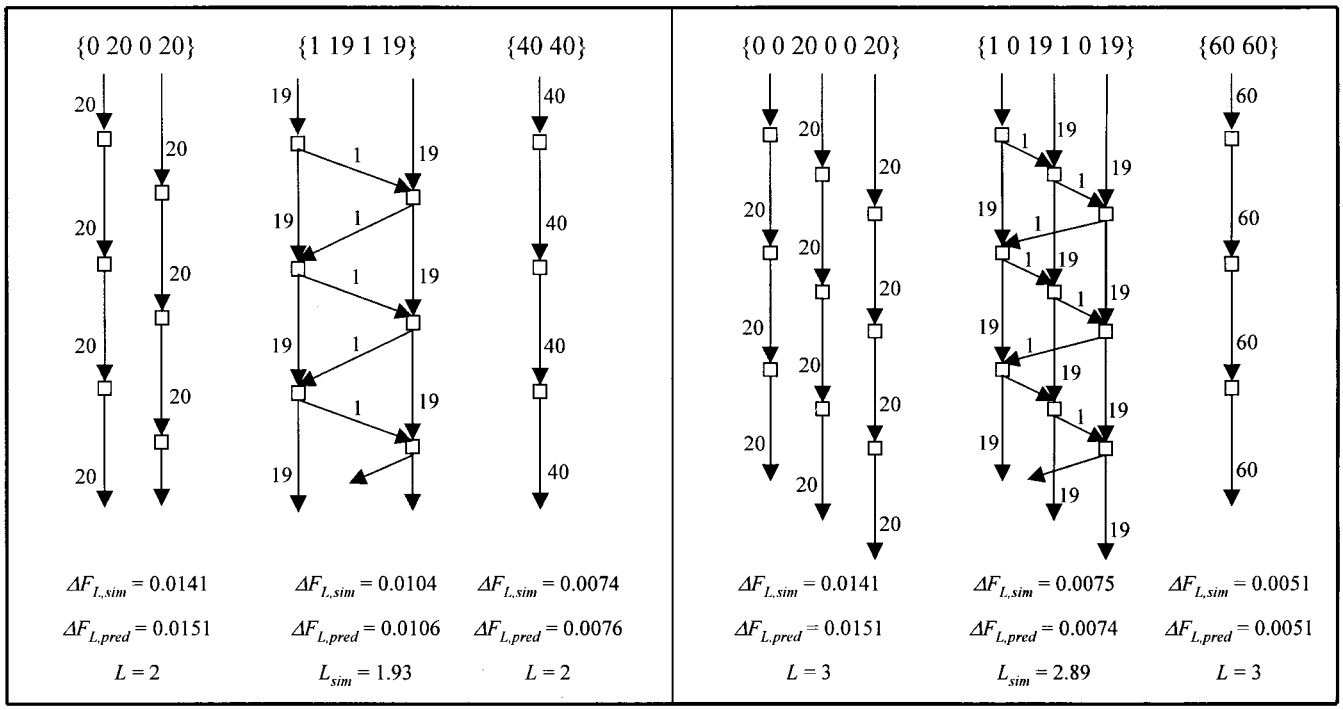

Figure 3.—Comparison between full line subdivision, partial migration, and one line, with an equal total number of parents per year. Numbers at lines represent the number of parents per sex, $h_0^2 = 0.4$, $n_o = 6$.

20, 0, 0, 20} and therefore the genetic variance is larger with full line subdivision.

Relationship between ΔF and heritability: Figure 4 shows the relationship between h_0^2 and ΔF_L, for two breeding schemes. The first scheme (S_1) has most parents in the first age class, **N** = diag{16, 4, 16, 4}, whereas the second scheme (S_2) has most parents in the second age class, **N** = diag{4, 16, 4, 16}. With S_1, ΔF_L has a maximum for $h_0^2 = 0.5$–0.6, similar to the discrete generation case (see Figure 1). With S_2, however, ΔF_L increases with heritability over the whole range. The increase of ΔF_L with h_0^2 for S_2 is mainly due to an increased contribution of parents in age class 1 at high heritabilities. With high heritability, genetic gain is large, which gives offspring of 1-year-old parents an increased selective advantage. This increases the contribution of parents in age class 1 relative to the contribution of parents in age class 2. For example, with S_2 and $h_0^2 = 0.5$, expected genetic contributions of average parents are α^T = [0.027 0.012 0.027 0.012], whereas for $h_0^2 = 0.9$, expected genetic contributions of average parents are α^T = [0.040 0.011 0.040 0.011]. This result shows that with increasing h_0^2 the genetic contributions become distributed more unequally over parents, resulting in a higher sum of squared contributions and therefore in an increased ΔF. Furthermore, with S_2, β increases with heritability, resulting in increased differences between genetic contributions of different parents selected from the same category, which further increases ΔF.

Rates of inbreeding per year can be obtained from

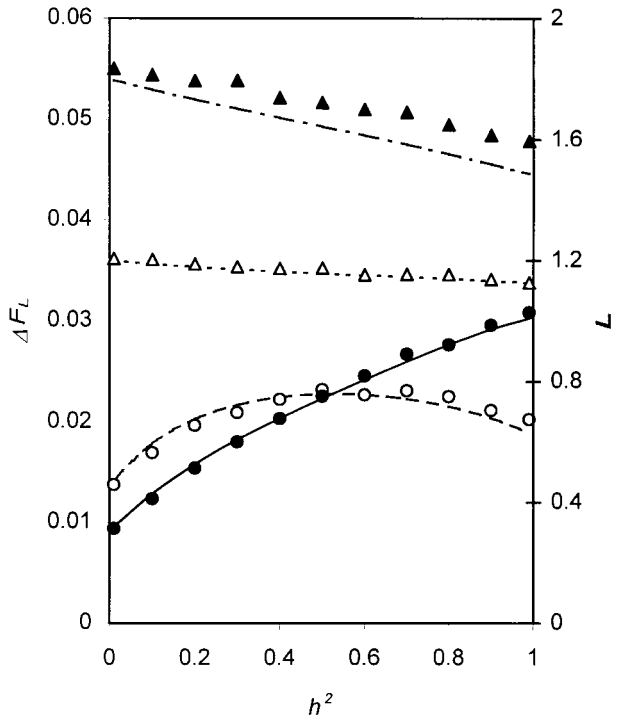

Figure 4.—Relation of heritability with simulated (symbols) and predicted (lines) generation interval (L) and with the rate of inbreeding per generation (ΔF_L), *with* $n_o = 8$, for two different breeding schemes, S_1, **N** = diag{16, 4, 16, 4} and S_2, **N** = diag{4, 16, 4, 16}. S_1: ○, $\Delta F_{L,sim}$; - - -, $\Delta F_{L,pred}$; △, L_{sim}; · · ·, L_{pred}. S_2: ●, $\Delta F_{L,sim}$; —, $\Delta F_{L,pred}$; ▲, L_{sim}; – - –, L_{pred}.

Figure 4 as $\Delta F_Y = \Delta F_L / L$, which shows the same trends with h_0^2 as ΔF_L. In conclusion, results from Figure 4 show that in contrast to the case of discrete generations, no general pattern can be observed in the relationship between ΔF and h_0^2 with overlapping generations.

DISCUSSION

Explicit prediction equations for rates of inbreeding in populations with either discrete or overlapping generations under mass selection were developed, on the basis of the approach of Woolliams and Bijma (2000) and Woolliams *et al.* (1999). Except for extreme selection intensities in females, predictions were accurate for discrete as well as for overlapping generations. Though based on a different approach, the current method extends the method of Nomura (1996) to populations with overlapping generations and an arbitrary distribution of parents across age classes, removing the stringent restriction of Nomura (1996). Relationships between rates of inbreeding and genetic and population parameters were also presented. General relationships apparent in discrete generations could not be extended to overlapping generations. For the prediction of rates of inbreeding in overlapping generations it is crucial to account for the inheritance of selective advantage both between and within categories. For discrete generations with only two categories (males and females), which do not compete for selection, only competition between selection candidates within categories is relevant.

The current method was compared to methods based upon the proportion of genetic variance transmitted to the offspring, which showed that with random mating, the equations of both Santiago and Caballero (1995) and Nomura (1996) can be reduced to simple expressions in terms of expected genetic contributions. Santiago and Caballero (1995) suggested that the differences between their results using the reduced genetic variance and those of Woolliams *et al.* (1993) using long-term contributions were due to the difference in approach. The present results show that the differences obtained previously were most likely due to errors in the derivations involving complex pathways over multiple generations that were needed by Woolliams *et al.* (1993). These complexities were avoided by Santiago and Caballero (1995). However, Woolliams and Bijma (2000) were able to derive the present results using long-term contributions by modeling the transfer of selective advantages in a single generation by assuming an equilibrium. The idea of basing the prediction on Bulmer's equilibrium variances was introduced by Santiago and Caballero (1995). However, their approach to modeling the inheritance of selected advantage by the proportion of genetic variance retained is correct only for mass selection [see Woolliams *et al.* (1999) for a general approach].

Prediction errors became large when the number of selection candidates per dam became extremely large (Figure 2), but these situations are out of the range of most artificial selection programs. Certain species (*e.g.*, fish or chicken) are able to produce many offspring per dam, but the number of selection candidates per dam is generally lower. High selection intensities in males can easily be obtained with a limited number of selection candidates per dam when the mating ratio is large. For these situations predictions were accurate (see Table 1, schemes with $d = 5$, $n_o = 8 \rightarrow i = 2.063$). The errors with large n_o were not present for low h^2 (results not shown), which indicates that the current method is also applicable to species with a large number of offspring when natural directional selection acts on a trait with low heritability.

In this article, equations for predicting rates of inbreeding were developed assuming a model of truncation selection on a normally distributed trait controlled by an infinitesimal model of gene effects. The predicted rate of inbreeding relates to homozygosity (by descent) at a neutral locus, unlinked to genes affecting the trait under selection (Woolliams and Bijma 2000). When the infinitesimal model does not hold, and the number of genes affecting the trait is large, or when the number of chromosomes is small, it is questionable whether neutral and unlinked loci exist at all. When loci are nonneutral, or linked to nonneutral loci, predicted rates of inbreeding cannot be related directly to the homozygosity at the locus, because a covariance between the genetic contribution and the gene frequency will arise due to selection (Woolliams and Bijma 1999). However, the rate of inbreeding can still be related to rates of inbreeding obtained by analyzing pedigrees using Wright's (1922) path coefficient method, or Malecot's (1948) coefficient of kinship, and also to estimates of inbreeding depression based on inbreeding levels calculated from the pedigree. Recently, Santiago and Caballero (1998) extended prediction methods for effective population size to populations with linked loci undergoing mass selection but for discrete generations only.

In general, to obtain accurate predictions of ΔF one needs to account for more than one generation of inheritance of selective advantage between categories. It was sufficient for Nomura (1996) to account for only a single generation because of the special case of equal numbers of parents per age class. In that case, shifting contributions between age classes has only a minor effect on ΔF because the contributions will remain with the same individuals with the same relative fitness, because every individual is selected in every category. Therefore the lifetime contribution will not be affected. For schemes where the number of parents differs between age classes, shifting of contributions between categories means shifting to other individuals (at least partly), which will affect the lifetime contribution. Consider, for example, scheme 10 in Table 2 with $h_0^2 = 0.5$:

accounting for only one generation of inheritance (*i.e.*, calculating $\boldsymbol{\alpha}$ from $\mathbf{N}\boldsymbol{\alpha} = \mathbf{G}^{\mathrm{T}}\mathbf{N}\boldsymbol{\alpha}$; Woolliams *et al.* 1999) gives $\Delta F_{\mathrm{pred}} = 0.0128$, an error of -21%; whereas using Equation 9 gives $\Delta F_{\mathrm{pred}} = 0.0159$, an error of only -2%.

The use of the concept of long-term genetic contributions to predict rates of inbreeding has several appealing properties. First, the derivation of the relationship between rates of inbreeding and genetic contributions is based directly on the probability of alleles being identical by descent, which enhances the intuitive understanding (Woolliams and Bijma 2000). Furthermore, rates of genetic gain can easily be obtained from the covariance between the genetic contribution and the Mendelian sampling component of the breeding value (Woolliams and Thompson 1994; Woolliams *et al.* 1999), which integrates methods for predicting genetic gain and rates of inbreeding. Finally, the prediction procedure for genetic contributions describes mechanisms determining the impact of current individuals on future populations and the turnover rate of genes and gives therefore an understanding of the mechanisms determining the development of the pedigree (Woolliams *et al.* 1999; Bijma and Woolliams 1999). Because the approach is general, it is clear how prediction equations can be extended to other situations.

With a fixed total number of parents selected per year, populations showed maximum rates of inbreeding (per year and per generation) when the number of parents entering the populations per generation was least, which occurred with an equal number of parents in every age class. Rates of inbreeding were smallest when most parents were in the older age classes, because those schemes had the largest number of parents entering the population per generation. This result broadly resembles the results of Hill (1974) for random selection in overlapping generations, although selected populations have an additional component of inbreeding arising from the expected differential contributions within age classes, which will modify this relationship. Schemes with most parents in the later age classes resembled population subdivision with some migration between lines. Because the selective advantage of categories depends on heritability, genetic contributions of categories are strongly affected when heritability changes (Bijma and Woolliams 1999); *i.e.*, contributions generally shifted to the younger age classes when heritability increased. Therefore, no general relationship between heritability and rate of inbreeding could be observed with overlapping generations.

In this article, equations were developed to predict rates of inbreeding for diploid populations with two sexes under controlled selection. The results are therefore primarily relevant for populations under artificial selection, for example, in animal breeding or in selection experiments. Though this article focuses on mass selection within age classes, results for mass selection across age classes can easily be accomplished by choosing the appropriate **N**, as in schemes 8 and 9 in Table 2. An extension to a situation where individuals in older age classes have more information, *e.g.*, progeny information, only requires the calculation of probabilities of selecting the same individual on different ages, which can be done using standard index theory. The method can also be extended to other selection strategies and modes of inheritance (*e.g.*, index selection and imprinting), using the key results of Woolliams and Bijma (2000) and Woolliams *et al.* (1999).

In animal breeding, optimization of breeding programs has focused for a long time on the maximization of genetic gain for the short term, partly because methods to predict long-term response were not available. When rates of inbreeding in selected populations can be predicted, predictions of long-term response under the infinitesimal model become available. This article enables methods for the optimization of breeding schemes on the long term (*e.g.*, Villanueva *et al.* 1996; Villanueva and Woolliams 1997) to be extended to populations with overlapping generations and mass selection.

J.A.W. gratefully acknowledges the Ministry of Agriculture, Fisheries and Food (United Kingdom) for financial support. Ab Groen is acknowledged for giving useful comments on the manuscript, and Tetsuro Nomura for generously sending us a copy of his programs. This research was financially supported by the Netherlands Technology Foundation (STW) and was coordinated by the Earth and Life Science Foundation (ALW).

LITERATURE CITED

Bijma, P., and J. A. Woolliams, 1999 Prediction of genetic contributions and generation intervals in populations with overlapping generations under selection. Genetics **151:** 1197–1210.

Bijma, P., J. A. M. Van Arendonk and J. A. Woolliams, 1999 Additional results and appendices to "A general procedure for predicting rates of inbreeding in populations undergoing mass selection." http://www.ri.bbsrc.ac.uk/geneflow/ (July 29 1999).

Bulmer, M. G., 1971 The effect of selection on genetic variability. Am. Nat. **105:** 201–211.

Burrows, P. M., 1984a Inbreeding under selection from unrelated families. Biometrics **40:** 357–366.

Burrows, P. M., 1984b Inbreeding under selection from related families. Biometrics **40:** 895–906.

Caballero, A., 1994 Developments in the prediction of effective population size. Heredity **73:** 657–679.

Falconer, D. S., and T. F. C. Mackay, 1996 *Introduction to Quantitative Genetics.* Longman, Essex, UK.

Fisher, R. A., 1918 The correlation between relatives on the supposition of Mendelian inheritance. Proc. R. Soc. Edinb. Trans. **52:** 321–341.

Hill, W. G., 1974 Prediction and evaluation of response to selection with overlapping generations. Anim. Prod. **18:** 117–139.

Hill, W. G., 1979 A note on effective population size with overlapping generations. Genetics **92:** 317–322.

James, J. W., 1987 Determination of optimal selection policies. J. Anim. Breed. Genet. **104:** 23–27.

James, J. W., and G. McBride, 1958 The spread of genes by natural and artificial selection in a closed poultry flock. J. Genet. **56:** 55–62.

Malecot, G., 1948 *Les Mathématiques de l'Hérédité.* Masson et Cie, Paris.

Meuwissen, T. H. E., and Z. Luo, 1992 Computing inbreeding coefficients in large populations. Genet. Sel. Evol. **24:** 305–313.

Nomura, T., 1996 Effective size of selected populations with overlapping generations. J. Anim. Breed. Genet. **113:** 1–16.
Pearson, K., 1903 On the influence of natural selection on the variability and correlation of organs. R. Soc. Lond. Phil. Trans. A **200:** 1–66.
Robertson, A., 1961 Inbreeding in artificial selection programmes. Genet. Res. **2:** 189–194.
Santiago, E., and A. Caballero, 1995 Effective size of populations under selection. Genetics **139:** 1013–1030.
Santiago, E., and A. Caballero, 1998 Effective size and polymorphism of linked neutral loci in populations under directional selection. Genetics **149:** 2105–2117.
Villanueva, B., and J. A. Woolliams, 1997 Optimisation of breeding programmes under index selection and constrained inbreeding. Genet. Res. **69:** 145–158.
Villanueva, B., J. A. Woolliams and B. Gjerde, 1996 Optimum designs for breeding programmes under mass selection with an application in fish breeding. Anim. Sci. **63:** 563–576.
Woolliams, J. A., 1998 A recipe for the design of breeding schemes, p. 427 in *Proceedings of the 6th World Congress on Genetics Applied to Livestock Production*, Vol. 25. Armidale, Australia.
Woolliams, J. A., and P. Bijma, 2000 Predicting rates of inbreeding in populations undergoing selection. Genetics **154:** 1851–1864.
Woolliams, J. A., and R. Thompson, 1994 A theory of genetic contributions, pp. 127–134 in Proceedings of the 5th World Congress on Genetics Applied to Livestock Production, Vol. 19, Guelph, Canada, pp. 127–134.
Woolliams, J. A., N. R. Wray and R. Thompson, 1993 Prediction of long-term contributions and inbreeding in populations undergoing mass selection. Genet. Res. **62:** 231–242.
Woolliams, J. A., P. Bijma and B. Villanueva, 1999 Expected genetic contributions and their impact on gene flow and genetic gain. Genetics **153:** 1009–1020.
Wray, N. R., and R. Thompson, 1990 Prediction of rates of inbreeding in selected populations. Genet. Res. **55:** 41–54.
Wray, N. R., J. A. Woolliams and R. Thompson 1990 Methods for predicting rates of inbreeding in selected populations. Theor. Appl. Genet. **80:** 503–512.
Wray, N. R., J. A. Woolliams and R. Thompson, 1994 Prediction of rates of inbreeding in populations undergoing index selection. Theor. Appl. Genet. **87:** 878–892.
Wright, S., 1922 Coefficients of inbreeding and relationship. Am. Nat. **56:** 330–338.
Wright, S., 1969 *Evolution and the Genetics of Populations. Vol. 2. The Theory of Gene Frequencies.* University of Chicago, Chicago.

Communicating editor: R. G. Shaw

APPENDIX A: DISCRETE GENERATIONS

Derivation of Equation 6: Starting from Equations 3 and 4, and substituting $\alpha_s^2 = 1/4N_s^2$, $\beta_s^2 = \alpha_s^2\lambda^2/(1-\pi)^2$, $\lambda = \frac{1}{2}i\sigma_P^{-1}$, $\pi = \frac{1}{2}(1-\kappa h^2)$, and $E[(A_{i,s} - \bar{A}_s)^2] = (1 - 1/N_s)\sigma_A^2(1-\kappa_s h^2)$, it follows that

$$E[u_{i,m}^2] = \frac{1}{4N_m^2} + \frac{1}{4N_m^2}\frac{i^2}{\sigma_P^2}\frac{(1-1/N_m)\sigma_A^2(1-\kappa_m h^2)}{(1+\kappa h^2)^2} + d\frac{1}{4N_f^2}\frac{i^2}{\sigma_P^2}\frac{(1-1/N_f)\sigma_A^2(1-\kappa_f h^2)}{(1+\kappa h^2)^2},$$

and

$$E[u_{i,f}^2] = \frac{1}{4N_f^2} + \frac{1}{4N_f^2}\frac{i^2}{\sigma_P^2}\frac{(1-1/N_f)\sigma_A^2(1-\kappa_f h^2)}{(1+\kappa h^2)^2} + \frac{1}{d^2}\frac{1}{4N_m^2}\frac{i^2}{\sigma_P^2}\frac{(1-1/N_m)\sigma_A^2(1-\kappa_m h^2)}{(1+\kappa h^2)^2}.$$

Substituting those expressions into $E[\Delta F] = \frac{1}{2}N_m E[u_{i,m}^2] + \frac{1}{2}N_f E[u_{i,f}^2]$ and using $\sigma_A^2/\sigma_P^2 = h^2$ and $d = N_f/N_m$ gives Equation 6.

Derivation of Equation 8: With a binomial distribution of family size, the deviation from a Poisson variance equals $np(1-p) - np = -np^2$, where n is the number of candidates ($\frac{1}{2}n_o d$ for sires and $\frac{1}{2}n_o$ for dams) and p is the selected proportion [$1/(\frac{1}{2}n_o d)$ for male offspring and $1/(\frac{1}{2}n_o)$ for female offspring]. Elements of $\mathbf{V}_{n(s)\text{dev}}$ are therefore $\mathbf{V}_{n(m)\text{dev}} = [-1/(\frac{1}{2}n_o d), 0; 0, -d/(\frac{1}{2}n_o)]$ and $\mathbf{V}_{n(f)\text{dev}} = [-1/(\frac{1}{2}n_o d^2), 0; 0, -1/(\frac{1}{2}n_o)]$. From $\delta_s = \boldsymbol{\alpha}^T\mathbf{V}_{n(s)\text{dev}}\boldsymbol{\alpha}$ it follows that $\delta_m = -1/[(\frac{1}{2}n_o d)(4N_m^2)] - d/[(\frac{1}{2}n_o)(4N_f^2)]$ and $\delta_f = -1/[(\frac{1}{2}n_o d^2)(4N_m^2)] - 1/[(\frac{1}{2}n_o)(4N_f^2)]$. The total correction equals $\frac{1}{8}N_m\delta_m + \frac{1}{8}N_f\delta_f = -1/(8n_oN_f) - 1/(8n_oN_f) = -1/(8T)$, where $T = \frac{1}{2}n_oN_f$.

Example. For $N_m = 20$, $N_f = 60$, $n_o = 8$, and $h^2 = 0.4$, selected proportions, selection intensities, and variance reduction coefficients are $p_m = 0.083$, $p_f = 0.250$, $i_m = 1.839$, $i_f = 1.271$, $i = 1.555$, $\kappa_m = 0.839$, $\kappa_f = 0.759$, $\kappa = 0.799$. Bulmer's (1971) equilibrium genetic variance and heritability are $\sigma_A^2 = 0.314$, $h^2 = 0.343$. From Equation 6 ΔF for a Poisson variance of family size equals $\Delta F_{\text{Poisson}} = 0.00625 + 0.00208 + 0.1277[0.02255 + 0.01212] = 0.01276$. From Equation 8, the correction equals $-1/1920 = -0.00052$ and the final prediction is $E[\Delta F] = 0.0122$.

APPENDIX B: OVERLAPPING GENERATIONS

Corrections for deviations of $\mathbf{V}_{n(k)}$ from Poisson variances: From Equation 1, the correction equals $\frac{1}{8}\mathbf{1}^T\mathbf{N}\boldsymbol{\delta}$, where $\boldsymbol{\delta}$ is a $2c_{\max}$ vector of elements $\delta_k = \boldsymbol{\alpha}^T\mathbf{V}_{n(k)\text{dev}}\boldsymbol{\alpha}$, and where $\mathbf{V}_{n(k)\text{dev}}$ is a $2c_{\max} \times 2c_{\max}$ matrix with deviations of $V_{n(k)}$ from Poisson variances (Woolliams and Bijma 2000). Similar to the case of discrete generations, deviations from Poisson variances are $-np^2$, where n is the number of candidates ($\frac{1}{2}n_o d$ for sires and $\frac{1}{2}n_o$ for dams) and p is the selected proportion. The selected proportion in subclass kl, *i.e.*, among offspring in category k descending from parents in category l, equals $p_{kl} = p_k g_{kl}/g_{1l}^0$, where p_k is the selected proportion in category k ($p_k = n_k/T$), and g_{kl} and g_{1l}^0 are elements of the modified gene flow matrix ($\mathbf{G}$) and the conventional gene flow matrix ($\mathbf{G}_0$), respectively. The element g_{kl} represents the proportion of *selected* offspring in category k descending from parents in category l, and g_{1l}^0 represents the proportion of candidates for selection in category k descending from parents in category l (Woolliams *et al.* 1999). Therefore, $\mathbf{V}_{n(l),\text{dev}}(k,k)$ equals $-\frac{1}{2}n_o d p_k^2 g_{kl}^2/[g_{1l}^0]^2$ when the parent is a male, and $-\frac{1}{2}n_o p_k^2 g_{kl}^2/[g_{1l}^0]^2$ when the parent is a female. Off-diagonal elements of $\mathbf{V}_{n(k)\text{dev}}$ are zero with binomial family size.

Example. For $\mathbf{N} = \text{diag}\{12, 8, 15, 25\}$, $h_0^2 = 0.4$, and $n_o = 4$, selected proportions, selection intensities, and variance reduction coefficients are $p = (0.1500\ 0.1000\ 0.1875\ 0.3125)$, $i = (1.5544\ 1.7546\ 1.4357\ 1.1331)$, $\kappa = (0.8051\ 0.8297\ 0.7877\ 0.7306)$. Predicted α, β, generation interval and Bulmer's (1971) equilibrium genetic

variance and heritability are (see Bijma and Woolliams 1999 for an example of the prediction of α and β) $\alpha^{T} = (0.01974\ 0.01454\ 0.01171\ 0.00710)$, $\beta^{T} = (0.02228\ 0.01829\ 0.01251\ 0.00904)$, $L = 1.416$, $\sigma^2_A = 0.3355$, $h^2 = 0.3586$. The conventional and modified gene flow matrices are (Bijma and Woolliams 1999)

$$\mathbf{G}_0 = \begin{bmatrix} 0.3 & 0.2 & 0.1875 & 0.3125 \\ 1 & 0 & 0 & 0 \\ 0.3 & 0.2 & 0.1875 & 0.3125 \\ 0 & 0 & 1 & 0 \end{bmatrix},$$

$$\mathbf{G} = \begin{bmatrix} 0.3245 & 0.1755 & 0.2291 & 0.2709 \\ 0.3276 & 0.1724 & 0.2347 & 0.2653 \\ 0.3227 & 0.1773 & 0.2258 & 0.2742 \\ 0.3180 & 0.1820 & 0.2175 & 0.2825 \end{bmatrix}.$$

For $\mathbf{N} = \text{diag}\{12, 8, 15, 25\}$ there are four *exclusive* categories: (1) males selected both at 1 and 2 years of age (*i.e.*, the eight highest-ranking males), for which $E[u^2_{i,s=1}] = E[(u^2_{i,k=1} + u_{i,k=2})^2]$; (2) males selected only at 1 year of age (*i.e.*, males ranking 9–12) for which $E[u^2_{i,s=2}] = E(u^2_{i,k=1})$; (3) females selected both at 1 and 2 years of age (*i.e.*, the 15 highest-ranking females), for which $E[u^2_{i,s=3}] = E[(u_{i,k=3} + u_{i,k=4})^2]$; and (4) females selected only at 2 years of age (*i.e.*, females ranking 16 through 25), for which $E[u^2_{i,s=4}] = E(u^2_{i,k=4})$. Summation of expectations of squares and cross-products over categories, s, gives, for males, $\Sigma^2_{s=1} n_s E(u^2_{i,s}) = 12\ E(u^2_{i,k=1}) + 8E(u^2_{i,k=2}) + 16E(u_{i,k=1}u_{i,k=2})$; and for females; $\Sigma^4_{s=3} n_s E(u^2_{i,s}) = 15E(u^2_{i,k=3}) + 25E(u^2_{i,k=4}) + 30E(u_{i,k=3}u_{i,k=4})$ (see also Equations 11 and 12).

From Equation 14,

$$E(u^2_{i,1}) = \alpha^2_1 - \left(1 - \frac{1}{n_1}\right)\beta^2_1\,\sigma^2_A(1 - \kappa_1 h^2) + d\left\{\overline{\alpha^2_f} - \overline{\alpha}^2_f + \sigma^2_A\overline{\left[\left(1 - \frac{1}{n_l}\right)\beta^2_l(1 - \kappa_l h^2)\right]_f}\right\}$$
$$= 0.0003897 + 0.0001086 + 0.0000606 = 0.0005589.$$

(Bars with subscript f denote averages over female categories weighted by the number of dams in the categories, *e.g.*, $\overline{\alpha^2_f}$ $(15 \times 0.01171^2 + 25 \times 0.00710^2)/40 = 0.829 \times 10^{-4}$. Similarly, for females $E(u^2_{i,k})$ is calculated from Equation 15. From Equation 16, $E(u_{i,3}u_{i,4}) = \alpha_3\alpha_4 + (1 - 1/n_3)\beta_3\beta_4\sigma^2_A(1 - \kappa_3 h^2) + \alpha_3\beta_4 E[\bar{A}_3 - \bar{A}_4] = 0.0000831 + 0.0000254 + 0.0000111 = 0.0001196$.

Using Equation 13 (note the reordering) with $\mathbf{N}_o = \text{diag}\{12, 8, 25, 15\}$ and

$$\mathbf{U}_o = E\begin{bmatrix} u^2_1 & 0 & 0 & 0 \\ 2u_1u_2 & u^2_2 & 0 & 0 \\ 0 & 0 & u^2_4 & 0 \\ 0 & 0 & 2u_4u_3 & u^2_3 \end{bmatrix} = 10^{-3}\begin{bmatrix} 0.5589 & 0 & 0 & 0 \\ 0.7868 & 0.3408 & 0 & 0 \\ 0 & 0 & 0.0946 & 0 \\ 0 & 0 & 0.2393 & 0.1972 \end{bmatrix},$$

the rate of inbreeding with Poisson family size is $E(\Delta F_Y) = \tfrac{1}{2}\mathbf{1}^T\mathbf{N}_o\mathbf{U}_o\mathbf{1} = 0.0123$. Instead of using the matrix form of Equation 13, one can also use $E(\Delta F_Y) = \tfrac{1}{2}\Sigma^{c\max}_{s=1} n_s E(u^2_{i,s}) + \tfrac{1}{2}\Sigma^{2c\max}_{s=c\max+1} n_s E(u^2_{i,s})$ with the summations calculated as above.

The correction for deviations of $\mathbf{V}_{n(s)}$ from Poisson variances, for sires in age class one to selected male offspring in age class two, is $\mathbf{V}_{n(1),\text{dev}}(2, 2) = -\tfrac{1}{2}n_o dp^2_2 g^2_{21}/[g^o_{11}]^2 = -0.0477$. The full matrix for sires in age class one equals

$$\mathbf{V}_{n(1),\text{dev}} = \begin{bmatrix} -0.1053 & 0 & 0 & 0 \\ 0 & -0.0477 & 0 & 0 \\ 0 & 0 & -0.1627 & 0 \\ 0 & 0 & 0 & -0.4389 \end{bmatrix}.$$

The matrices for other age classes are $\mathbf{V}_{n(2),\text{dev}} = \text{diag}\{-0.0692, -0.0297, -0.1105, -0.3235\}$, $\mathbf{V}_{n(3),\text{dev}} = \text{diag}\{-0.0672, -0.0313, -0.1020, -0.2629\}$, $\mathbf{V}_{n(4),\text{dev}} = \text{diag}\{-0.0338, -0.0144, -0.0541, -0.15957\}$. $\boldsymbol{\delta}^T = [-9.554\ -6.474\ -6.004\ -3.168] \times 10^{-5}$, *e.g.*, $\delta_1 = \boldsymbol{\alpha}^T\mathbf{V}_{n(1),\text{dev}}\boldsymbol{\alpha} = -9.554 \times 10^{-5}$. The correction factor is $\tfrac{1}{8}\mathbf{1}^T\mathbf{N}\boldsymbol{\delta} = 0.0004$, resulting in $\Delta F_Y = 0.0123 - 0.0004 = 0.0119$ and $\Delta F_L \approx L\Delta F_Y = 0.0168$.